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EFFECT OF MUSCULAR ACTIVITY ON CONDITIONED SECRETORY REFLEXES IN MAN

Fiziologiya nervnykh protsessov [Physiology of Nerve Processes], 1955, Kiev, Pages 438-449

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The study of the higher nervous activity of animals was placed on an objective foundation by the method of conditioned salivary reflexes originated by I. P. Pavlov. No other method aspiring to objectivity can compare to it in this regard. Therefore, while Pavlov was still alive Lents and Smirnov used the method of conditioned secretory reflexes to study the higher nervous activity of healthy human adults as well. Despite the fact that Pavlov did not regard this absolute imitation of animal experiments as fully valid, many physiologists have employed and still today employ his classic method in the study of the laws of nerve processes in the child, as well as in the healthy and sick adult.

This can perhaps be explained by the fact that to this day there is no universally accepted method for studying the higher nervous activity in man. On the other hand, while the fundamental mechanisms of the higher nervous activity, discovered in studies of conditioned reflexes in animals, also apply to man, Pavlov always warned against simply transferring data from the animal to the human sphere. In this regard, K. M. Bykov has written that "human activity involves a number of specific factors which cannot be given due consideration in a simplified analysis based solely on

data obtained with dogs," and believes it necessary to establish a new method for the study of the activity of the human brain.

Today, no method completely satisfactory for human studies has yet been devised. Therefore, objective and properly-grounded conclusions with regard to various phenomena of human cranial activity can be obtained only if this judgment is based on the study of human cortical processes not merely by one, but by a number of methods.

This methodologically multifaceted approach to the study of any given manifestation of higher nervous activity in man must employ as one of its means the investigation of conditioned secretory reflexes.

G. V. Fol'bort and associates have determined the basic laws of the occurrence and interaction of the processes of exhaustion and recovery fundamental to the processes of fatigue and rest. The development of this direction of study is currently in the stage of the investigation of the processes of exhaustion and recovery in the cerebral cortex. Under Fol'bort's guidance we are presently doing research on the interrelation between the processes of excitation and inhibition in human muscular activity, and toward that end we are employing a number of methods.

In full consciousness of the fact that an effort to apply to man the results of research on the conditioned reflexes of dogs cannot be successful, we nonetheless decided to supplement the material we had previously collected by undertaking a study of the conditioned reflexes of man in muscular activity.

Method

Conditioned secretory reflexes were investigated in a study of the cranial activity of man in muscular activity. Saliva from the parotid gland was withdrawn in a plexiglass capsule (designed by Krasnogorskiy, Levin, and Klorin). The amount of saliva secreted was determined by the Ganike-Kupalov method (passage through water and air, one drop corresponding to 3 gradations on the scale, and 40 drops to one cu cm). The number of drops was recorded by kymograph, whereby a drop falling on the Ganike instrument closed an electric circuit and was recorded on a smoked tape by an electrically-operated needle.

Cranberry juice of constant concentration served as the unconditioned stimulus. The unconditioned stimulus was applied for 30 seconds, during which time the subject drank 8 to 10 cm^3 of cranberry juice. The positive conditioned reflexes employed included a quiet bell, the lighting of a 50-w electric bulb, the lighting-up of a red square, a metronome at 180 beats to the minute (this stimulus was used for differentiation with 2 of the subjects), and the conditioned stimulus "I am giving you the cranberry juice." The differentiation stimuli were the lighting-up of a green square, and a metronome at 90 beats to the minute (this stimulus was positive with 2 subjects).

When the reflexes had been elaborated, and differentiation fixed, the effect of muscular activity thereon was tested. In other instances a study was made of the effect of muscular activity on the process of elaborating conditioned reflexes. The effect of muscular work was also tested in cases in which, despite the considerable number of combinations, the conditioned reflexes remained inconstant.

The conditioned swallowing reflex was studied simultaneously with the conditioned secretory reflexes. The method of air transmission developed by N. I. Krasnogorskiy was employed to record swallowing.

The muscular activity consisted of pedalling a stationary bicycle carrying a load differing for each subject. The difficulty of the work was determined by taking the pulse and measuring respiration and perspiration. The subjective attitude of the subject to the work was determined, the units of effort applied were calculated, and aeroenergographic data were taken into account. The method of aeroenergographic recording has been described by Zhuravlev and Kudryavtsev. (The subject is told to squeeze a rubber bulb, the compression being recorded by a kymograph operated by the air in the bulb. A Richardson bulb and pressure gauge are used to establish the desired pressure in the system, thus providing the resistance needed for compression by hand). We asked the subjects to squeeze the bulb with utmost strength and frequency until no longer able to do so. The subject was asked to do this before pedalling the stationary bicycle, again immediately after finishing that work, and subsequent to rest thereafter. In view of the results of the experiments of Zhuravlev and Kudryavtsev, who noted a rise in work capacity after limited work, and a decline after much work, we believed that these aeroenergograms would help us determine the difficulty of the work performed.

On the basis of the various indices listed above we classified the work performed by the subject as light, medium, and heavy, for the individual concerned. Our subjects were students, school pupils, and technical personnel, 10 in number. A total of

301 experiments were run, of which 105 investigated cerebral activity during muscular work.

Results of the Research

We were convinced ourselves at the very outset of the difficulty of elaborating conditioned secretory reflexes in man. Our first experiments, with subjects O. G. and L. D., produced no conditioned reflexes even after 100 or more combinations of stimuli. Losing hope of elaborating conditioned reflexes in the usual way, we asked one of our subjects to try to think about the conditioned reflex when it appeared, giving attention to its taste and color. This did produce reflexes on 2 or 3 occasions, but as they failed to become constant, we temporarily dropped the experiments as vacation time had come. When work with these subjects was renewed the latter showed precise reflexes for a short period, but thereafter the reflexes appeared and disappeared irregularly.

Developing conditioned reflexes in subject L. N. proved equally difficult. In her case, it took more than 30 combinations. With the rest of the subjects, conditioned reflexes appeared after 10 to 15 combinations. With certain individuals the conditioned reflex first appeared to light stimuli, and then to sound (P.V.), while with others it was just the opposite (S. T.). The conditioned reflex appeared more rapidly to the oral stimulus ("I am giving you the cranberry juice") than to the others. With the subjects who developed conditioned reflexes rapidly, relative stability of these reflexes was evident from the seventh or eighth experiment, while in subject O. G. this stability was obtained only in the thirtieth experiment, her reflexes being clearly defined from the thirtieth to the thirty-seventh experiments,

thereafter (and thus to the end of the study) alternately appearing and failing to appear. Conditioned secretion in subjects L. M. and L. D. was likewise alternating in its appearance. With regard to the remaining subjects, it is also impossible to speak of clearly-defined conditioned reflexes, although some degree of constancy was nonetheless to be observed. True, toward the end of the observations, even relative constancy was lacking in virtually all the subjects, and the reflexes were lacking in a number of cases.

In the majority of subjects, differentiation was elaborated after 3 to 5 experiments in which reinforcement was not used.

The magnitude of the reflex was small in all subjects, even those in whom the reflex was distinct. In the majority of the subjects the conditioned reflex represented 3 to 5 gradations on the scale, reaching 10 to 15 only in the case of S. T. In addition, the unconditioned stimulus produced an adequate secretory effect.

Figure 1 presents kymographic records of the conditioned reflex. Here (subject Kh. M.), the conditioned secretion consisted of 3 drops of saliva, preceded somewhat by a motor reaction, swallowing. A combined study of the swallowing reflex and the secretory reaction showed inconstancy in this reflex reaction as well. In a number of cases this reflex was clearly defined, in which case the swallowing motions preceded the conditioned reflex, but in the majority of experiments, the conditioned reflex for swallowing was absent. Krasnogorskiy and Shastin believe that the motor reactions must be regarded only as supplementary, in view of their lack of constancy.

In order to increase the secretory effect somewhat, we decided to increase the excitability to food of 3 subjects. We thus requested them to take neither dinner nor supper before the experiment. The rule was for the subjects to participate in the experiment before breakfast. However, if the experiment were to be performed during the second half of the day, the last intake of food was not to be less than 5 hours before the experiment. After the experiment the subject was given breakfast in the laboratory. Our observations of these subjects showed more constant conditioned reflexes than in others, but this constancy was disturbed thereafter, and the reflexes began to disappear. Questions to the subjects elicited the information that, despite the artificial induction of hunger, they had never thought about food, although other thoughts had often occupied them.

Our preliminary work in the elaboration of conditioned human secretory reflexes may be summed up as follows. In man, conditioned, artificially-induced reflexes are not stable and easily disappear on repetition. The magnitude of the conditioned reaction is low and irregular. Only a large amount of experimental data makes possible the discovery of a relationship between the magnitude of the reaction and the use of any given stimulus. Differentiation was easier to obtain and was more constant. S. T. was an exception in this regard; she failed to reveal differentiation.

On the basis of the foregoing standard, which is not fully precise, we nonetheless proceeded to study conditioned reflexes of secretion during muscular activity. In 2 instances we began our

research was also [illegible] elaboration of conditioned reflex.

Our observations showed that muscular activity facilitates a more precise manifestation of conditioned reflexes and differentiations, and more rapid formation thereof. But this series of observations was likewise characterized by lack of constancy in the manifestation of conditioned reactions. In a number of experiments very precise results were observed, but on other occasions the findings, under identical conditions and with the same subjects, were different, and we could thus not be confident of the conclusion drawn on the basis of the prior experiment.

All the data we obtained are generalized in the accompanying table. In compiling it, we distinguished, to begin with, the findings resulting from different types of work: with light, average, and muscular loads respectively. Then, in each series of observations and for each experiment, we determined strengthening, weakening, or failure of the conditioned reflex to show change. The same procedure was followed, as concerns differentiation.

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Difficulty of work	Total No of expts	Conditioned reaction				Differentiation			
		Strengthened	Weakened	No change	Unclear	Strengthened	Weakened	No change	Unclear
Light	28	18	-	10	-	1	10	17	-
Medium	40	23	8	9	-	-	13	12	15
Heavy	37	30	20	-	11	6	15	7	9
		(at outset)	(at end)						
		2	4						

Of 28 experiments with light muscle load and different subjects, the data in the table show that there was an increase in the conditioned reflexes in 18 experiments, and no change in the remaining 10. We noted no weakening of the conditioned reflexes to light work. Light muscular activity disorganized differentiation in 10 experiments. In 17 experiments the reaction remained unchanged, and in one it was strengthened.

In work of medium difficulty, the conditioned reflex also showed an increase in the majority of cases (23 of 40 experiments), while differentiation was weakened in 13 experiments. On the other hand, in 8 experiments of medium difficulty, the conditioned reflexes were weakened.

In 20 of 37 experiments involving severe muscular activity the table shows that the result was an increase in the conditioned secretion only at the beginning of the observation, while at the end the reflexes declined. In 4 experiments with heavy muscular activity a weakening in the conditioned reflexes was observed throughout the entire experiment, and in 2 cases the reflexes increased throughout the experiment. On heavy work, differentiation was disorganized in 15 experiments, while in 6 it increased.

The difficulty of muscular work was determined in accordance with a number of indices, but it was always difficult to make accurate allowance for such a factor as the attitude under which the work was performed. Therefore, in a number of instances the possibility that work of medium difficulty could become heavy, and vice versa, cannot be excluded. It is possible that it is specifically this which explains the fact that in 8 experiments

with work of medium severity the reflexes became weaker, while in 2 with heavy work they were always at a high level.

Having thus grouped our data in a table, and having found in a majority of instances definable principles, we believed it possible to advance selected experiments which would confirm the principle inherent in each, although the number of those precise experiments constitute only a third of our total number of observations.

Figure 2 presents an experiment, subject L. N. The illustration shows clearly the strengthening of conditioned reflex activity in light muscular activity. Before this work, her reaction to the metronome, at 90 beats, was one drop of saliva at the sixty-first combination, and 2 drops in response to the red square at the twenty-ninth try. Her conditioned secretion increased during the performance of work. Four drops were secreted in response to the lighting of the lamp on the first try, 3 drops on the thirty-second try to the red rectangle, and 2 to the 90-beat metronome at the sixty-second combination of stimuli. After rest, the conditioned secretory reaction again showed a decline, one drop of saliva being secreted in response to the 90-beat metronome at the sixty-third combination.

In a number of cases the conditioned swallowing reflex was manifested clearly, in which situation it preceded the secretory reaction. In the majority of cases, however, the swallowing reaction set in only in response to the unconditioned stimulus.

In addition to the graphic record, the secretory reaction was noted in the gradations of the scale. In the experiment shown

In Figure 3, the gradations are indicated by the height of the columns in the diagram (subject B. S., female). Prior to performance of work, the conditioned reaction to light, metronome, and bell was 3 gradations on the scale, and differentiation was complete. During work of medium difficulty the conditioned secretion increased 2- or 3-fold (8 gradations on the scale to the thirteenth combination of stimuli including the lamp, 12 gradations at the fourteenth, and 9 gradations at the fifteenth. Differentiation was markedly disordered (saliva secretion to 180 beats of the metronome being 5 gradations at the sixteenth combination of stimuli, and 10 gradations at the seventeenth). After 15 minutes of rest, the magnitude of the conditioned reflexes declined, but not to its initial value.

In the majority of cases heavy muscular activity elevated the secretory reaction only at the beginning of the experiment, its magnitude declining thereafter. Figure 4, showing Experiment 8 with subject V. Kh., shows this effect. Prior to work, the nineteenth combination of stimuli including the lamp showed the conditioned secretory reaction to be 7 gradations on the scale. After 6 minutes of work, secretion of saliva to that stimulus constituted 8 gradations on the scale, but only 2 after 35 minutes, and 3 after 45 minutes. The 180-beat metronome yielded a 5-gradation reaction before work, 5.5 after 11 minutes of work, 7.5 after 19 minutes, and 2 after 49 minutes.

Summary

Before proceeding to explain the results we had obtained, we should like to offer our views on the method employed. The

method of conditioned secretory reflexes is useful in studying certain manifestations of the higher nervous activity in man. Conditioned reflexes of secretion are often developed, it is true, with great difficulty, the strength of the inhibitory process thus making itself felt.

One is struck by the irregularity of the conditioned reflex, and by its disappearance, for which no explanation immediately presents itself. We were unable to determine any precise connection between these phenomena and either happenings in the lives of the subjects, or their state of mind, or even with food excitability, although in a number of instances such a relationship clearly existed. Experiments set up against the background of the uninterrupted reading of books by the subjects presented interesting results. In these cases the conditioned secretory reaction emerged more clearly. The conditioned reaction also appeared with greater clarity on performance of light muscular activity.

As long ago as when Lents demonstrated the first conditioned secretory reflexes, it was observed by V. Yu. Chagovets that the major obstacle with respect to the observation of conditioned secretion in adults is the mass of inhibitory factors mixed in, in which it is very difficult to orient oneself.

R. P. Ol'nyanskaya, studying the influence of the cerebral cortex on gas metabolism, also ran into irregularity in the course of conditioned human reflexes. She found the conditioned reflexes to be well-defined when first formed, but subsequently vanishing from observation. K. M. Bykov explains this disappearance by the fact that excitation of individual portions of the cortex, due,

for example, to the fixing of attention, inhibits other portions, as well as subcortical centers, by the mechanism of negative induction.

In our experiments it is possible that mild muscular activity or the reading of books distracted the subject's attention from some previously dominant thought, and this removed induced inhibition from the center of salivary secretion, facilitating improved manifestation of the reaction. Our observations by the method of conditioned secretory reflexes were limited solely to a study of certain elementary manifestations of the higher nervous activity in man.

The results of our observations show that muscular activity affects the course of conditioned reflexes in man, depending upon the severity of the work. Mild muscular work strengthened the secretory reflexes in every case. Medium work also increased the conditioned reflexes in the vast majority of cases. Heavy work strengthened conditioned reflexes only during the first 5 to 10 minutes.

The inhibitory processes remained unchanged, or were weakened, as the foregoing occurred.

It may be assumed that muscular activity, mild, average, or even heavy, also elevated the excitability of the cerebral cortex (heavy work doing so only at the outset), thus facilitating the reinforcement of conditioned reflexes.

In a number of experiments with medium work loads we found no strengthening but, instead, a weakening of the conditioned

secretory reflexes. This weakening was almost always observed toward the end of heavy work. In 4 cases in which heavy work was engaged in, the reflexes were observed to weaken from the beginning to the end of the experiment.

It may be that heavy and, to some degree, medium muscular activity concentrated excitation in the motor analysor, and that this had the capacity to induce a weakening in the activity of other departments of the cerebral cortex.

Muscular activities of differing intensities resulted either in disturbing differential inhibition or in failure to affect it. Only in very heavy work (in 6 experiments) did differentiation grow stronger. To verify this fact, we tested the strength of the inhibitory process in a number of experiments by extending the period of differentiation. These tests showed that in muscular activity of light and medium severity, long-continued activity of the differential stimulus serves as a rule to disturb differential inhibition, this disorder usually setting in after 20 seconds of activity by the stimulus. In a number of experiments in heavy work, differentiation proved to be disordered prior to and subsequent to work, and even at its beginning. However, at the end of the period of work, not one drop of saliva was secreted, despite the long-term action of the differentiating stimulus. Figure 3 (subject V. S., male), is an example of such an experiment. The data shown in the diagram show that prior to work (I), after the differentiating stimulus had been operative for 36 seconds, 3 drops of saliva were secreted, i.e., differentiation was disinhibited. However, during very heavy work (II), differentiation was complete, despite the fact that the stimulus operated for 60

seconds. After rest (III), 52 seconds of operation of the negative stimulus again led to disruption of differentiation, 3 drops of saliva being secreted. Usually, with this subject, the application of the differential stimulus for 20 seconds yielded complete differentiation.

Our tests of the strength of the inhibitory process, showing its strengthening in severe muscular activity, may be explained by the development of exhaustion in the motor analysor, due to work uninterrupted for a long period of time. To protect nerve cells from exhaustion, a process of defensive inhibition sets in, and irradiates to the entire cerebral cortex.

The aeroenergograms we studied may be taken as very remote and questionable confirmation of this hypothesis. Let us remember that the muscular activity consisted of pedalling a bicycle. The major load therefore fell on the legs and torso, the hands hardly participating in the work and no aeroenergogram being recorded by the hands. The aeroenergogram was of greater magnitude in work of medium severity, and also in heavy work, with persons accustomed thereto. Very heavy work showed a reduction of magnitude in the aeroenergogram. Figure 6 shows the aeroenergogram for subject O. G. (female) after work of medium and high severity on the stationary bicycle. The aeroenergogram record was taken at 3 stages: before work (I), immediately after work (II), and after 20 to 25 minutes of rest (III). Work of medium intensity on the stationary bicycle brought an increase in the aeroenergogram: before work the subject compressed the bulb 52 times in 45 seconds; after work 53 times in 36 seconds; and after 26 minutes of rest, 52 times in 49

seconds. Thus, after work of medium intensity, the subject compressed the bulb more intensely than before and after work on the stationary bicycle. On the other hand, hard work on the bicycle, as shown in the lower portion of the drawing, led to a reduction of the intensity of work with the hands. Before the work and after rest, the aeroenergogram showed 47 squeezes. Before work these compressions took 39 seconds; after work they took 40.5 seconds. But in the second stage, immediately after very heavy work, the subject squeezed the bulb only 46 times in 43.5 seconds.

Compression of the bulb is a voluntary act, the impulses for which come from the motor area of the cerebral cortex. Fundamental nervous processes are set up in this analysor on the performance of muscular work. It may be hypothesized that in muscular activity of medium and mild severity it is the stimulatory process which predominates, which is why the aeroenergogram shows an increase in the work done by the hand. In heavy work on the bicycle, the long-term concentration of the stimulatory process in the motor zone results, in the long run, in exhaustion of the nerve cells and development of defensive inhibition, the result of which is a decline in the number of voluntary compressions of the bulb by the hand.

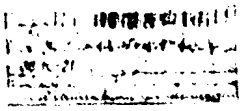

Figure 1. Recording of conditioned secretion and conditioned swallowing in man. Top to bottom: drops of saliva secreted (3 drops in response to the conditioned stimulus, and 56 to the unconditioned); swallowing motions. The conditioned stimulus is identified by letters, and the number signifies that it was being applied for the twenty-first time. The next line indicates application of the unconditioned stimulus (the giving of cranberry juice), while at the bottom there is a time scale divided into 3-second units.

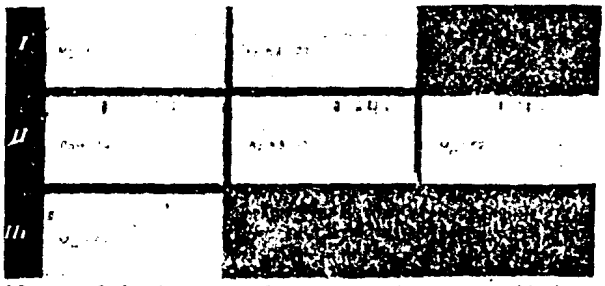

Figure 2. Effect of light muscular activity on conditioned secretion in man. I, conditioned secretion and swallowing prior to muscular activity; II, same, during muscular activity; III, same, after 30 minutes of rest. The significance of each line is the same as in Figure 1.

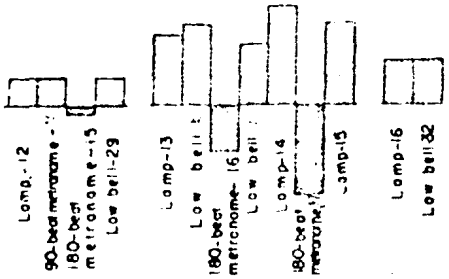

Figure 3. Effect of muscular activity of medium severity on conditioned reflexes of secretion in man. Key: The columns with diagonal lines represent the conditioned secretory reaction; the columns with cross-hatched lines represent differentiation; the letters signify the conditioned stimulus; the adjacent numbers, the number of experiments in which the given stimulus was applied: A, before performance of work; B, during work; C, after work.

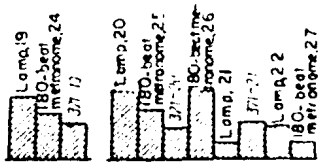

Figure 4. Effect of heavy muscular activity on conditioned secretion in man. A, before work; B, during work. Remaining symbols are same as in Figure 3.

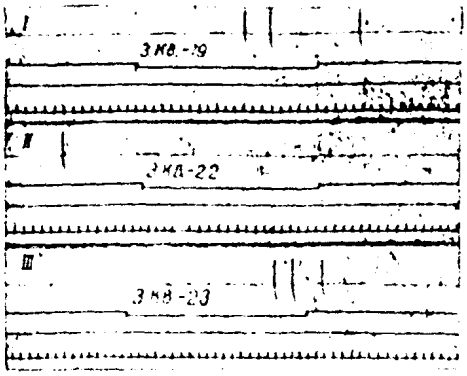

Figure 5. Effect of heavy muscular activity on the strength of the inhibitory process. I, record of secretory action before work; II, record of secretory action 35 minutes after start of heavy muscular work on stationary bicycle; III, after 20 minutes of rest. Key to lines, top to bottom: first, secretion reaction; second, differential stimulus; third, unconditioned stimulus; fourth, time scale, 3-second gradation.

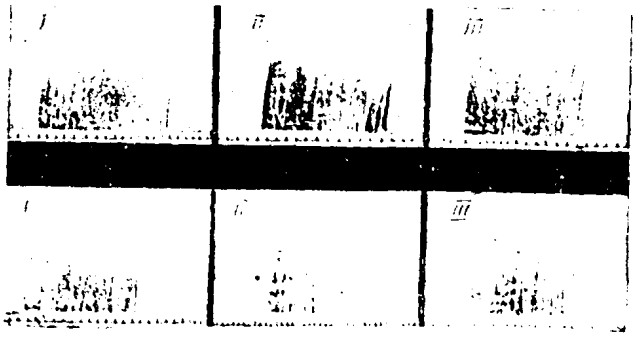

Figure 6. Effect of muscular activity of varying intensity on aeroenergogram. I, record of aeroenergogram prior to work on stationary bicycle; II, immediately after work; III, after 20 minutes of rest. Top portion of drawing: during work of medium severity; lower portion: during heavy work. Significance of lines: first, record of aeroenergogram (compression of rubber bulb by hand pressure); second, time scale, 3-second gradations.